

Effect of Head Tilt on Visual Cortical Cell Function in the Intact and Labyrinthectomized Cat

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The area of the receptive field, its length and width, its position in the visual field, the peristimulus time (PST) histogram (i.e., the response to successive moving light-bar stimuli), the directional preference, the velocity gradient, and the intertrial (spontaneous) firing rate were studied electrophysiologically in complex cortical visual cells in Brodmann's area 18. These characteristics were explored after head tilt, in immobilized cats, both in intact and in bilaterally labyrinthectomized animals. In intact animals (in 64 cells), most of these characteristics changed after head tilts of 10, 20, 30, or 40° to the right or to the left of the horizontal plane. There was always one specific head position in which the receptive field area was at its smallest. In labyrinthectomized animals (in 29 cells), the lengths, widths, and the areas of the receptive fields were only minimally altered during identical tilts. Similarly, in the labyrinthectomized cats, head tilts (40°, to the right or left) caused no substantial changes in the shape and duration of the PST histogram, compared with those in intact cats. No two visual cortical cells responded to head tilts in exactly the same manner. Such uniqueness in response is probably of importance during visual image analysis; in particular, as it relates to cortical reconstruction of stable visual images during continuously changing head movements and positions. © 1986 Academic Press, Inc.

INTRODUCTION

The reconstruction and recognition of the virtual visual image in the visual area of the cerebral cortex is a problem discussed mainly by theoreticians

Abbreviation: PST—peristimulus time.

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who have proposed various hypothetical models based on single-cell feature extraction, spatial frequency analysis, and so forth [for review see (24)]. Unfortunately, an analysis of single-cell activity provides little opportunity for constructing a meaningful model of the activities of a larger neuronal system, or the whole visual area.

In particular, the issue of perceptual object constancy during changing conditions of observation, when the object is rotated, shifted, or recedes in distance, or when the observer moves his head and eyes and still is able to recognize the identity of the object, has seldom been approached by experimenters who try to correlate activities of visual cortical neurons with the visual input.

A mechanism by which perceptual constancy can be achieved during movements of the head might depend, among others, on the interactions of the visual and vestibular systems. This was first demonstrated in the crayfish by Wiersma and Yamaguchi (29). There is some evidence that, in other animals, the interaction between visual and vestibular systems may also serve to achieve visual perceptual constancy. Studies indicate that peripheral vestibular activation modifies the firing rate of cells in the visual cortex, the superior colliculus, and the lateral geniculate body (4, 13, 19). In a number of cortical cells in the cat, the angle of preferred stimulus movement has been altered by changes in the orientation of the head (2, 6, 15, 27). Body tilt has also been reported to affect the size and shape of the receptive field in some cells (6) as well as the "spontaneous" firing rate (28). The size and position of the receptive field, as well as its orientation within the visual field, have been shown to be influenced by head tilt as well (11). Furthermore, a nystagmogenic agent, deuterium oxide (heavy water), mimics some of these effects in animals whose heads are maintained in a stable position (20, 21).

In this study the modifications in several receptive field characteristics of visual cortical cells in cats after head tilt were examined electrophysiologically. As opposed to other authors who studied (mainly) simple cell properties (27), our work was confined to a study of the complex cell properties in area 18 of the cortex. After a short pilot study (in which the extreme variability of the responses of the visual cortical cells to the vestibular activation was recognized), we simplified the analysis by concentrating the effort only on the complex visual cells. It was felt that complex cells may receive a varied input from various intrinsic and extrinsic sources, and thus, they might exhibit greater influence from the vestibular input. In order to establish the role of vestibular sensory input in the mediation of the studied changes, the effects of head tilt were also examined in bilaterally labyrinthectomized animals.

METHODS

Animal Preparation and Experimental Protocol. Thirty-one adult cats (2.5 to 4.0 kg) were used; 10 were bilaterally labyrinthectomized prior to recording.

Details of the labyrinthectomy and the preparation were published elsewhere (8, 21, 26).

A T-shape block was attached to the skull of all animals prior to recording. Because the animal was clamped to the stereotaxic apparatus by this block, the need for eye and ear bars was eliminated.

Just before the recording, the animal was prepared for the experiment under halothane anesthesia. The animal was immobilized with pancuronium bromide (0.013 mg/kg), the halothane-oxygen anesthesia was terminated, and artificial ventilation was immediately begun. The nictitating membrane was retracted with ophthalmic Neosynephrine, and the pupils dilated with atropine sulfate. Contact lenses were installed, with additional, separate artificial pupils (4 mm diameter).

The stereotaxic apparatus was modified so that the animal's head and an electrode holder could be smoothly rotated around the caudorostral axis of the body to positions 40° (in 10° increments) right or left of horizontal. In each of the nine head positions, the optic discs and at least two large retinal blood vessels were projected directly and plotted on a tangent screen, by a dark-adapted experimenter. The screen was then covered with Albanene tracing paper, and situated 81 cm in front of the corneal surfaces. These projections provided reference points from which eye movements could be determined during tilt. Repeated plotting of the optic discs showed that the residual eye movements, if present, were within limits of the method of manual plotting on the screen and could not contribute substantially to the changes described in this paper which were greater at least by one order of magnitude.

The area centralis was estimated ophthalmologically, but the absence of clear-cut retinal features made these projections somewhat uncertain; therefore, their positions were also calculated by a method which uses binocular receptive field pairs separated on the tangent screen after the extraocular muscles have been paralyzed (1, 17, 18). The calculated position, in most cases, closely coincided with the geometric projection of the visual axis of the eye.

To establish a suitable reference system for estimating the position of the receptive fields of studied cells, a line was drawn connecting the center of the projected optic disc and the projection of the area centralis of the eye. The position of each receptive field within the visual field was determined in relation to this "meridian" (see Fig. 1). The two measures used for this purpose were the perpendicular distance from the appropriate meridian to the geometric center of the receptive field (length "A" in Fig. 1), and the distance between the projected visual axis and the intersection of length A with the meridian (i.e., length "C" in Fig. 1).

The length of the meridian remained constant when the head was tilted contralaterally to the tested eye. However, when the head was tilted ipsilaterally to the eye, there was a linear increase in meridian length with tilt magnitude.

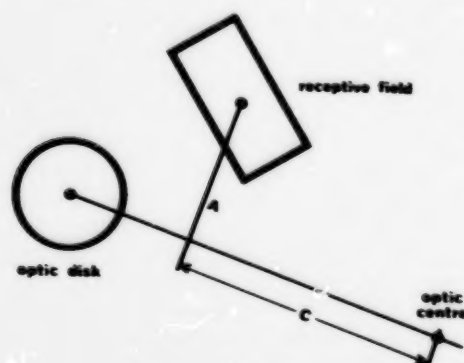


FIG. 1. Schematic diagram showing the reference points used to calculate some of the receptive field characteristics on the tangent screen. The projected optic center and the center of the projected optic disc are connected by a line (the "meridian"). The length of the perpendicular line drawn from the meridian to the geometric center of the receptive field provides the position reference measure defined as "A." The length of the meridian from its intersection with A to the projected optic center is the position reference referred to as "C." A separate meridian connecting the projection between the optic center and optic disc had to be redrawn each time the receptive field was plotted in each tilt orientation.

This suggests that some of the effects on the receptive field characteristics, which have been attributed to head tilt, may have been caused by orbital geometry and the shifting of the eye within the eye socket. However, one factor precludes that possibility; viz., that the maximum change in the meridian length was only 2.5%, which is well within the margin of error allowed for the analysis of other variables. A correction of the meridian length during ipsilateral tilts was made in the calculations of the receptive field positions.

Electroencephalographic activity, heart rate, core temperature, and expired carbon dioxide were monitored. Body temperature was stabilized at $38 \pm 0.5^\circ\text{C}$. The state of sleep and alertness was determined regularly from the electroencephalogram. All precautions were taken to eliminate pain and distress. The friendly behavior of the animals toward the experimenters between experimental sessions showed that the precautions taken were successful. Moreover, all phases of these experiments were approved by the Canadian Council on Animal Care after their careful analysis and repeated on-site inspections of the procedures used for animal treatment.

Data Acquisition and Treatment. Single cell activity was recorded with Epoxylite-coated tungsten microelectrodes and conventional amplification. A digitized record of the unit activity was obtained by a pulse-height discriminator (Nicolet, model 1074) to drive an electronic counter.

The receptive field of an isolated unit was plotted on a tangent screen using slits of light, usually not more than 2° long, produced by a hand-held ophthalmoscope. Sheets of paper on the plotting screen provided a permanent record of the position and shape of the receptive fields. The light bar was swept over the outer limits of the receptive field from one long side of the field, and then from the other. These limits are substantially influenced by the length of the light bar, and therefore, were kept as close as possible to the 2° limit. Then, the short sides of the receptive field were plotted using, first, short light bars parallel to the long axis of the receptive field, and then, much longer light bars suitable for the recognition of the inhibitory end-zones of the hypercomplex cells. The short ($<2^\circ$) light bars were used for the determination of the short side of the excitatory area of the receptive field. Finally, the length of the light bar was adjusted to correspond to the length of the long axis of the field, and the path on which it was able to excite the cell was plotted. This length was termed the optimal length of the receptive field. This term must not be confused with the optimal stimulus length as determined, e.g., by Kato *et al.* (9). The path on which this light bar was able to activate the cell was called the width of the receptive field.

The complex and hypercomplex cells were then distinguished once more, during the recording of the peristimulus time (PST) histogram, where a 13.3° long light bar was used which invariably activated the inhibitory end-zone of the hypercomplex cells.

To distinguish the simple cells from the complex cells, the response of the cell to the stationary flashing light was used (in addition to determining the length of the field and its inhibitory flanks). Simple and hypercomplex cells were excluded from the final evaluation of the data.

After plotting and other tests (described later) were completed, the animal's head (but not the body) was tilted in 10° increments to one side. The receptive field was replotted in each orientation. The head was then returned to the horizontal, and the receptive field plotted again. Receptive field lengths and widths were then plotted for the same tilt positions in the other direction. Finally, the head was returned to the horizontal and the receptive field was plotted a third time. This method served as a test of the reproducibility of the repeated plots of the same receptive field (12). The tilt itself was rather slow, about $1^\circ/\text{s}$, and was interrupted always when the firing of the studied cell was disappearing in the background noise. Therefore, some of the tilt sequences were incomplete. Then, it was usually possible to return to the horizontal position and start in the other direction. In cases of uncertainty, i.e., when it was not certain that recordings from the same cell took place, all data were discarded.

In addition to the plotting of receptive fields, the spontaneous activity, the orientation selectivity, and the velocity gradient were also quantified. Spon-

taneous activity was recorded in the presence of the background illumination of the screen, and prior to plotting the receptive field dimensions at each head tilt. A period of 15 min was always sampled.

PST histograms to the moving light-bar stimuli were also recorded (10-ms bins, 100 sweeps). The stimulus was a light bar, 0.2 by 13.3°, back-projected onto the tangent screen with sweep velocities between 2 and 28°/s. The path of the light bar was 24° long. Because of the different speeds of the moving light bar, the length of the bins differed from 0.02 to 0.28°.

The optimal stimulus orientation of complex cells is often less well defined than in simple cells. Therefore, the orientation tuning curves were obtained at 24 orientations, at 15° increments by moving the light bar perpendicular to its long axis at a speed of 12°/s at 10-s intervals. For each orientation, ten sweeps were summed, and the intertrial spontaneous activity was subtracted.

There is a continuous transition between cells lacking distinct orientation tuning and cells with a narrow angle of responsiveness. Therefore, the overall shift of the response of the complex cell to lines at different angles was analyzed with a method derived from a hierarchical clustering technique as described in detail elsewhere (21). The responses to all orientations of the moving light bar were taken into consideration, and the orientation shift calculation was based on the least-squares fit to the original tuning curve (Euclidean distance between datasets). In short, the individual responses (numbers of spikes) of the cell to 24 different bar orientations were considered variables which, together, formed one dataset. The dataset recorded when the animal's head was in the horizontal position was compared with the dataset after the most extreme (40°) tilt, in order to assess whether or not the directional preference of the cell had changed in response to tilt.

For this purpose, a matrix of 24 sets of directional preferences was created, using the dataset for the horizontal position. All of its 24 values were rotated (shifted), one by one, so that the cell's response was shifted by 15°. This process was repeated 23 times, and the Euclidean distances between the set of responses of the cell after the 40° tilt and the 24 pretilt datasets were calculated.

The rotated set giving the smallest Euclidean distance would be the one most similar to the posttilt dataset; its position, therefore, was an indication of the posttilt orientation selectivity shift of the cell. The BMDP program P2M (hierarchical cluster analysis of cases) was used for this analysis (3).

Changes in optimal stimulus velocity were sought by obtaining velocity tuning curves for the range from 2 to 28°/s. The speed at which the light bar gave the largest response was taken as the optimal speed.

Finding a well isolated cell with suitable electrophysiologic characteristics and its testing often lasted for more than 10 h. Therefore, no more than one cell was recorded during a single experimental session. Fortunately, each an-

imal could be used for six to eight recording sessions spaced at 2-week intervals. The locus of each electrode was recorded in stereotaxic coordinates. At termination of each session, the cranial defect was filled with a small quantity of sterile bone wax, and the skin was sutured; after recovery from the Pavulon immobilization, the animal was returned to its cage. Antibiotics were administered prophylactically.

At termination of the last experimental session, the animal was euthanized with Pentothal, and perfused with physiologic saline and then 10% buffered Formalin. The electrode position was ascertained from the records of the stereotaxic coordinates and the traces of their penetration. Only cells that were reliably localized within area 18 are described.

RESULTS

Sixty-four (64) cells from cats with intact labyrinths, and 29 cells from labyrinthectomized animals were studied. Length, width, and area of the receptive fields were measured in all cells (see Table 1). The number of cells which were used in determining the other characteristics, such as orientation selectivity, PST histogram, and velocity gradient, varied according to the time that a cell could be held for recording.

Changes in the Length of the Receptive Field. The length of the receptive field of most of the visual cortical cells changed whenever the animal's head was tilted. Both increases and decreases in length were observed. When the responses from all cells were combined, the average length increased 16% when the animals with intact labyrinth were tilted from the horizontal position to either of the extreme positions. In this, as well as in the other analyses described in this paper, the data from both right and left tilts were pooled, because an analysis of variance of all values in the individual tilted positions, as well as *t* tests for the extreme (40° tilt) values indicated that no statistically

TABLE 1
Length and Width of the Receptive Fields for Intact and Labyrinthectomized Cats*

	Intact				Labyrinthectomized			
	Horizontal position		Minimal-dimension position		Horizontal position		Minimal-dimension position	
Length	6.39	2.26	3.63	1.66	7.48	3.36	7.21	3.25
Width	3.75	1.31	2.64	0.93	3.51	0.95	3.55	1.01

* Values are $\bar{x} \pm SD$ degrees of visual angle.

significant difference existed between them. Also, there were no significant differences between the cells driven from the contralateral and ipsilateral eye. These average values, however, did not sufficiently characterize the real changes in the receptive field length, because both gradual increases and decreases of the optimal length were summed in them.

In one of the nine tilted head positions, the receptive field of each cell always had its shortest length; and, from that position to all others, the length gradually increased. The positions at which the individual cells showed their shortest receptive fields were more or less evenly distributed throughout all nine tilt positions, according to a chi-square test ($P < 0.25$).

Because of this finding, the data were related to the minimal length of the receptive field for each particular cell. Figure 2 indicates that, the farther the head was tilted away from the "minimal-length position" for the cell, the greater the length of the receptive field became. The changes were very robust and could not be overlooked when the receptive field was plotted on the screen. This gradual increase was highly significant ($P < 0.0001$, analysis of variance).

When the data obtained from intact and labyrinthectomized animals were compared, several striking differences were found. The maximal mean percentage change in the length of the optimal line to tilt in the labyrinthectomized

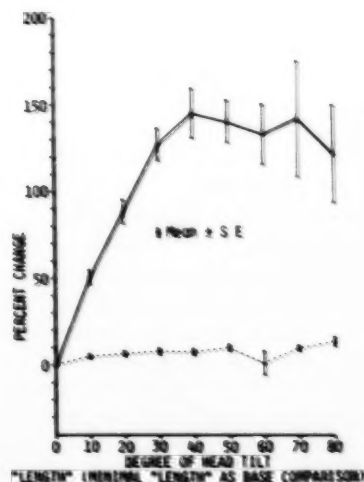


FIG. 2. Mean $\pm$ SE percentage change in the optimal length of the light bar stimulating the visual cortical cells in Brodmann's area 18 during head tilt. All values are related to the "minimal-length position," i.e., the position of the head at which the cell responded to the shortest optimal line. Intact cats (—); labyrinthectomized cats (---).

animals did not exceed 4%. In labyrinthectomized animals, the chi-square test ($P < 0.25$) indicated that the "minimal-length positions" of individual cells were also evenly distributed with tilt. If the cells were further evaluated according to the "minimal-length positions," the subsequent increases were still not greater than 13% (see Fig. 2). Compared with intact animals, this increase was significantly smaller (analysis of variance, $P < 0.01$).

Another statistically significant finding was that the average receptive field in the minimal-length position was twice as long in labyrinthectomized animals as in intact animals (Student's t test, $P < 0.001$).

The "Width" of the Receptive Field. As with the optimal length, the "width" increased in intact cats, on the average, from the horizontal position toward both extreme positions. The average increases were, however, not statistically significant, with the exception of the extreme (40°) position, in which the difference in relation to the horizontal position was significant ($P < 0.05$, Student's t test for dependent variables). In labyrinthectomized animals, the average change did not exceed 2% of the original width. The differences between the intact and labyrinthectomized animals were statistically significant (analysis of variance, $P < 0.01$).

In a manner analogous to the comparison used above utilizing the minimal-length position, the minimal-width position could be used as a basis for comparisons. When this was done, the increase during tilts in both directions became much more prominent in the intact cat. However, in the labyrinthectomized animal, the differences still remained very small. These data are summarized in Fig. 3. A two-way analysis of variance between the intact and labyrinthectomized cats showed a significant difference between the two groups ($P < 0.01$).

As with the length, the width of the receptive field was larger in labyrinthectomized animals than in intact ones; and this difference was highly statistically significant (Student's t test for independent variables, $P < 0.001$).

There was no one single position of the head at which the minimal "width" prevails, in either intact or labyrinthectomized cats (chi-square test, $P < 0.25$). In many cells, the minimal-width position coincides with the minimal-length position. The frequency of this coincidence, compared with chance distribution, was statistically significant (chi-square test, $P < 0.01$).

Receptive Field Area. The "area of the receptive field" was calculated as a rectangle, one side of which was the length of the receptive field, the other, the path on which the bar was able to optimally stimulate the cell. This obvious relation is stressed here because a careful observer may, after evaluating several receptive fields, notice that the true receptive field is usually not a rectangle. Both the intact and labyrinthectomized groups demonstrated a gradual increase in the average receptive field area with increasing head tilt. However, this increase was significantly more pronounced in the intact group (analysis

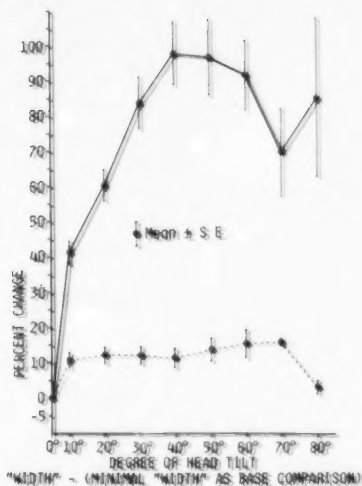


FIG. 3. Mean $\pm$ SE percentage change in the "width" of the receptive field, relative to the "minimal-width position," i.e., the position of the head at which the cell responded to the smallest swept "width" of the optimal length of the stimulus. Intact cats (—); labyrinthectomized cats (---).

of variance, $P < 0.01$). Examples of the plots of the receptive fields of an area-18 complex cell during all tilts in both an intact and a labyrinthectomized cat are presented in Fig. 4.

As with the other dimensions, the receptive field areas were evaluated in relation to the position having the smallest one (Fig. 5). This position often, although not always, coincided with the position of "minimal length" and "minimal width." In cats with intact labyrinths, mean percentage changes from the "minimal area" position were as large as +400%. The distribution of the minimal-area position for all tilts in both the intact and labyrinthectomized cats (Table 2) indicated that, in the labyrinthectomized animals, the minimal-area position coincided with the horizontal head position more often than in the intact animals. This relationship was statistically significant (chi-square test, $P < 0.005$). The average area of the minimal receptive field in the intact group also differed significantly from that in the labyrinthectomized group (Student's t test, $P < 0.05$). In the labyrinthectomized cats, the receptive field areas were generally larger.

The increase in the receptive field area of the labyrinthectomized animals during tilts was small, and usually less than 15% (Fig. 5). In the intact group, on the contrary, the increase in the area with tilt was considerable. The differences between labyrinthectomized and control animals were, again, highly

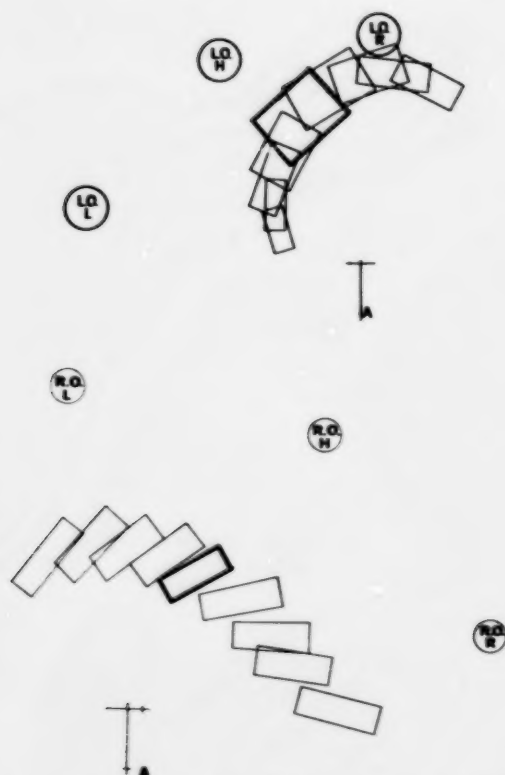


FIG. 4. An illustration of the areas and positions of the receptive field of cell 133-1 (top; intact cat), and cell 138-1 (bottom; labyrinthectomized cat), two complex visual cortical cells in area 18, seen in the horizontal position (rectangle with thick lines) and after tilts to the right and to the left. Abbreviations: L.O.H.—projected optic disc in the horizontal position, L.O.L.—optic disc at the 30° left tilt, L.O.R.—projected optic disc at 30° right tilt, A—axis of rotation of the animal.

statistically significant in all tilt positions (two-way analysis of variance, $P < 0.01$).

The receptive field areas tended to be more elongated in labyrinthectomized animals. The shape of the receptive field was calculated as a ratio of the "width" and "length" of the field. The difference in this ratio between labyrinthectomized and intact animals was significant, both in the horizontal position (Student's *t* test, $P < 0.05$) and in the "minimal-area position" ($P < 0.001$).

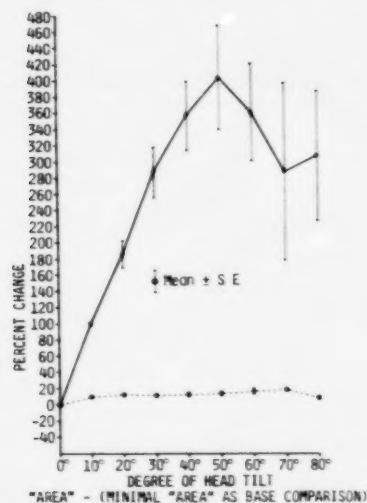


FIG. 5. Mean $\pm$ SE percentage change in the receptive field area as a function of head tilt, in both the intact (—), and labyrinthectomized (---) groups. For each cell, the head position which corresponded to the smallest receptive field area was defined as its "minimal-area-position" orientation. The area obtained for each cell in each tilt orientation was then expressed as a percentage of the area determined in the "minimal-area-position" orientation.

Receptive Field Position. Changes in the position of the receptive field during head tilts were drawn by a computer-aided graphics program (5) in such a way that length "A" was plotted on the x axis, and length "C" on the y axis of the plot (see Fig. 1). These plots were equivalent to superimposing all meridian plots on C. Of the 38 cells from intact animals in which data were available for all positions, the relative position of the receptive field in the visual field did not substantially change in 22 cells. During the tilts from 0 to 40°, both to the right and left, the centers of these receptive fields moved in different directions, but only over a relatively small area, which had a diameter of $3.5 \pm 0.9^\circ$ ($\bar{x} \pm SD$) for right tilts and $3.0 \pm 1.2^\circ$ for left tilts (see Fig. 6). These values were probably within the limits of measurement error.

In eight other cells, the receptive fields drifted considerably from their original positions when the head was tilted. The average shifts of the receptive field centers were 15.7 ± 13.8 and $11.5 \pm 13.9^\circ$ for the right and left 40° positions, respectively. An example of such a shift is presented in Fig. 7. The remaining group of eight cells showed a linear shift of the receptive field with tilts to one side or the other, and none with tilts to the opposite side.

In the labyrinthectomized animals, changes in the receptive field positions were evaluated in 18 cells. Seven showed only minor shifts of position (3.8

TABLE 2

Distribution of the "Minimal-Area Position" According to the Position of the Head for 0°, and Left and Right Tilts, for Both Intact and Labyrinthectomized Cats*

Tilt condition (°)	Status of cat	
	Intact	Labyrinthectomized
Left tilt		
40	5	0
30	11	0
20	8	4
10	7	6
Horizontal		
0	3	9
Right tilt		
10	10	2
20	6	4
30	8	2
40	6	2

* Values are number of observations; see text for details.

± 0.7 and $2.6 \pm 0.7^\circ$ with 40° tilts to the right and left, respectively). Six of the others showed a linear shift of the field during the tilts ($9.1 \pm 6.0^\circ$ during right tilts and $8.2 \pm 2.4^\circ$ during left tilts). In five cells, there was only a unilateral shift ($9.2 \pm 4.4^\circ$), with no shift after head tilt to the opposite side.

So, in both intact and labyrinthectomized animals, there were some cells in which the receptive fields shifted, in relation to the visual field of the eye

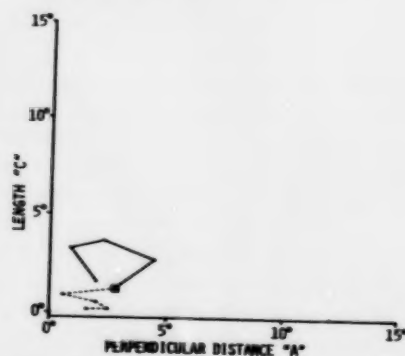


FIG. 6. Path of the receptive field position of cell 155-2 (intact cat) during tilts to the right (—) and to the left (---). ■, Horizontal position. See Fig. 1 for definition of "A" and "C."

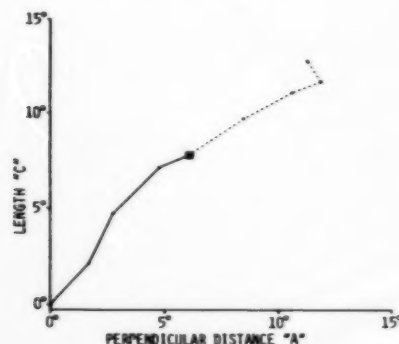


FIG. 7. Path of the receptive field position of cell 152-3 (intact cat) during tilts to the right (—) and to the left (---). ■, Horizontal position. See Fig. 1 for definition of "A" and "C."

and its landmarks, when the animal's head was tilted. The magnitude of these shifts exceeded anything possible from changes in the geometry of the eye.

The position of the shifting fields within the visual field was not related to its distance from the area centralis. The cells with both shifting and nonshifting visual fields were evenly distributed throughout the visual field of the eye.

Changes in Optimal Stimulus Orientation. The variability in the orientation selectivity of complex cortical cells was rather high. Cells with no orientational tuning were found (which were excluded), as well as cells with a very narrow range of orientation selectivity. The responses of 16 cells to a right tilt of 40° and 15 cells to a left tilt of 40° were evaluated in a group of cats with intact labyrinths. In the labyrinthectomized cats, responses to right tilts were tested in 8 cells and to left tilts in 9 cells. The shifts in the selectivity, summarized in Fig. 8 for both intact and labyrinthectomized cats, indicated that there were changes due to head tilt; but these changes are rather variable, and each cell responded in its own unique way. In the figure, the values around zero show that the orientation selectivity of the cell did not substantially change during the tilt; and was, therefore, shifted only by the amount of the tilt. Values around 45° and 315° indicate that the cells compensated for the tilt; i.e., they preserved the same directional preference in relation to gravity, in spite of the tilt. However, several cells overreacted to the tilt, or even changed their directional preference in the direction of the tilt.

Figure 9 shows examples of the changes in the directional preferences of two visual cortical cells of area 18 after tilts of the head 40° to the right and to the left.

Changes in Velocity Gradient. Data from intact animals were available from 12 cells, 6 of which were studied in the horizontal position and at a 40°

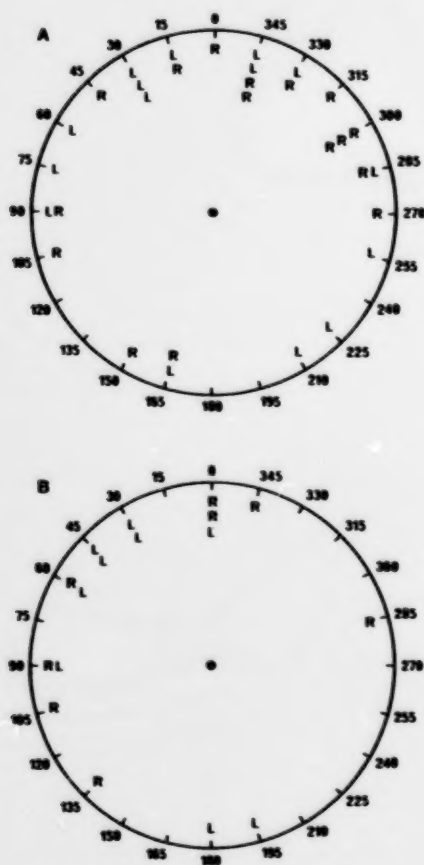


FIG. 8. Polar plots illustrating the overall shifts in the orientational selectivity of area-18 visual cortical cells in intact (A) and labyrinthectomized (B) cats, after tilts of 40° to the right (R) and the left (L). The values are compared with the directional preference of the same cells in the horizontal position (i.e., at 0°) using an Euclidean distance of measure, a least-squares clustering technique. The position of R and L describes the shift of the orientational selectivity after the tilt.

right tilt, and 6 in horizontal and 40° left positions. In 7 of these cells, the optimal velocity in the horizontal position was originally within the range of tested speeds, relatively high, and it decreased after the tilt. In the remaining cells, the optimal velocity in the horizontal position was originally low, and increased because of the tilt (Table 3). No statistical evaluation was carried

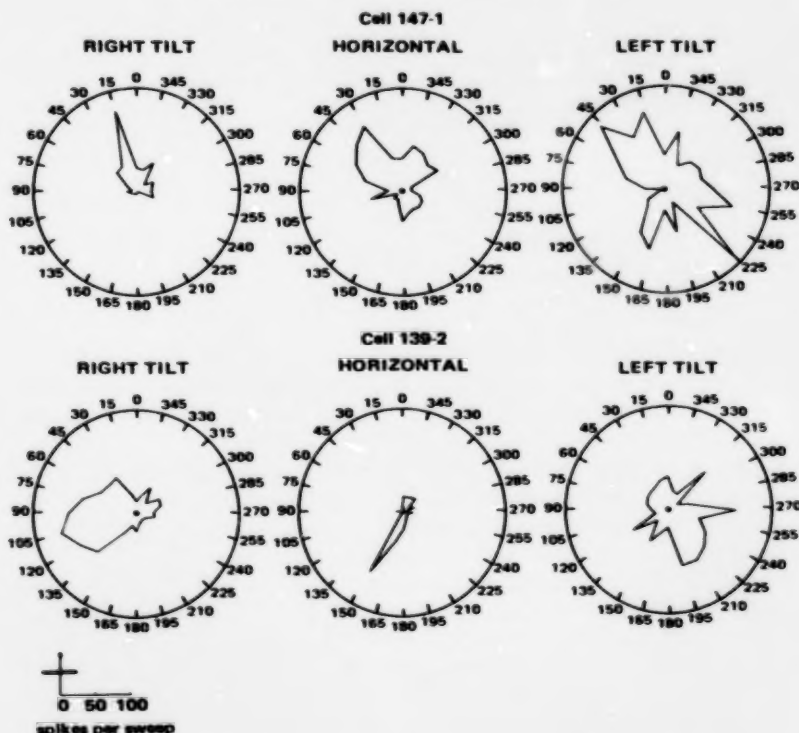


FIG. 9. An example of the tilt-induced changes in the directional preferences of cell 147-1 and cell 139-2 from intact cats to 40°-right and 40°-left tilts. The ● defines the center of the polar plot.

out, due to the small number of observations and the wide distribution of the data.

The Peristimulus Time histograms. A PST histogram of the visual cortical cell, taken while the animal's head was in the horizontal position (0°), was compared with one taken while the head was tilted 40°. Recordings from 23 cells in intact cats were obtained for extreme right tilts, and 19 for extreme left tilts. The duration and shape of the main wave usually changed after tilt. In all cases, changes in the duration of the main wave corresponded with altered widths of the cell's receptive fields. The data could be divided into two groups: one showing an increase in the duration of the wave, the other no change or a slight decrease (Table 4). These data were compared with the mean value for the horizontal position. The increase in duration after tilt was

TABLE 3

Optimal Velocity of Light Bar Required to Activate Area 18 Visual Cortical Cells before (0°) and after 40° Head Tilt in Cats with Intact Labyrinths^a

Group	N	Velocity at 0° (°/s)	Velocity at 40° tilt (°/s)
High-velocity	7	17.14 ± 2.96	8.14 ± 2.12
Low-velocity	5	4.00 ± 0.46	14.00 ± 0.51

^a Values are $\bar{x} \pm SE$.

significantly different from that obtained before tilt (*t* test; right tilt: $N = 15$, $P < 0.001$; left tilt: $N = 9$, $P < 0.01$). The decrease in duration after tilt was not statistically significant (see Table 4). Examples of these changes are shown in Fig. 10.

In the labyrinthectomized cats, no substantial alteration in the shape and duration of the PST histogram was seen with tilt (10 cells, right tilt; 9 cells, left tilt). This finding may be correlated with the absence of any change in the receptive field in labyrinthectomized cats during the tilts.

Spontaneous Activity. The "spontaneous" activity, i.e., the activity of cells being stimulated by the background illumination, regularly changed when the animal's head was tilted by 10° to a new position. Before the first tilt, the rate of spontaneous activity was 54.85 ± 56.51 ($\bar{x} \pm SD$) spikes per minute in intact and 87.64 ± 65.35 spikes per minute in labyrinthectomized animals. The difference between these two values was not statistically significant. During the actual tilting movement, which was rather slow (1°/s), the activity usually

TABLE 4

Changes in the Duration (in seconds) of the Peristimulus Time Histogram before (0°) and after 40° Head Tilt in Cats with Intact Labyrinths

Tilt	Group	N	At 0°		To 40° tilt		Student's <i>t</i> test
			Mean	±SD	Mean	±SD	
Right	All	23	1.76	0.64	1.96	0.68	NS
	Increase only	15	1.52	0.52	2.28	0.56	$P < 0.001$
	Decrease only	8	1.68	0.68	1.36	0.60	NS
Left	All	19	1.59	0.61	2.08	1.00	NS
	Increase only	9	1.52	0.68	2.74	1.04	$P < 0.01$
	Decrease only	10	1.96	0.58	1.52	0.60	NS

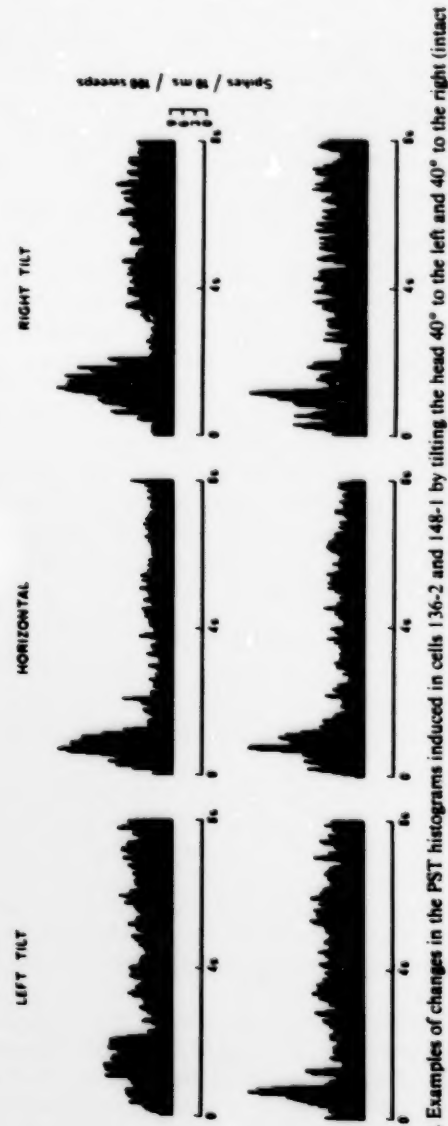


FIG. 10. Examples of changes in the PST histograms induced in cells 136-2 and 148-1 by tilting the head 40° to the left and 40° to the right (intact cats).

increased suddenly. This change may have been associated not only with the vestibular, but also with the visual stimulation while the head was actually moving. After the head was fixed in the new position, the cell activity gradually subsided and remained at a new level. Both increases and decreases in the spontaneous activity occurred after the tilt (see Fig. 11). There were also some changes in labyrinthectomized animals, but they were generally less intensive than the changes in intact animals.

Although the other variables examined herein returned to their original values when the head returned to the horizontal position, the spontaneous activity showed considerable volatility. In most cells, the spontaneous activity recorded during a 15-minute period in the horizontal head position before the tilt, after the tilt and the return, and after the second tilt and the return to the horizontal, differed substantially. Because of this, the changes in the spontaneous activity were related to the rate of spontaneous activity immediately preceding the tilt. This method yielded more consistent data than evaluating the absolute firing rates in each head position. Whenever the animal's head was tilted by 10°, the spontaneous activity changed in a rather regular manner (see Table 5). These alterations were present both in labyrinthectomized animals and in intact ones; there was a statistically significant difference between intact and labyrinthectomized animals only during the actual tilting process (Student's *t* test, $P < 0.05$).

DISCUSSION

This paper describes the changes which occur in the receptive field properties of complex cells in area 18 of the cerebral cortex in the cat when the head is tilted. The most important finding is that all, or nearly all, complex cells are sensitive to head tilt.

Another important finding concerns the extreme variability of the response of individual neurons to tilt, which made statistical evaluation and generalization of the data very difficult. When all these characteristics are considered, each cell is seen to respond in its own way. This uniqueness in the cellular characteristics is often overlooked when the function of the visual system and, perhaps, of the entire brain, is considered. Nonetheless, it is probably of critical importance in the analysis of the visual image, particularly during movements of the head and body.

These findings support the observations made in a previous study (21), in which the vestibular system was stimulated both galvanically and by injection of a nystagmogenic substance, deuterium oxide. Taken together, the effects of heavy water, head tilt, and galvanic stimulation demonstrate the visual cortical cell activity is functionally modified by the vestibular system.

In view of the small, but obvious effects of tilt in labyrinthectomized animals, the effects of head tilt on certain receptive field characteristics result, to a very

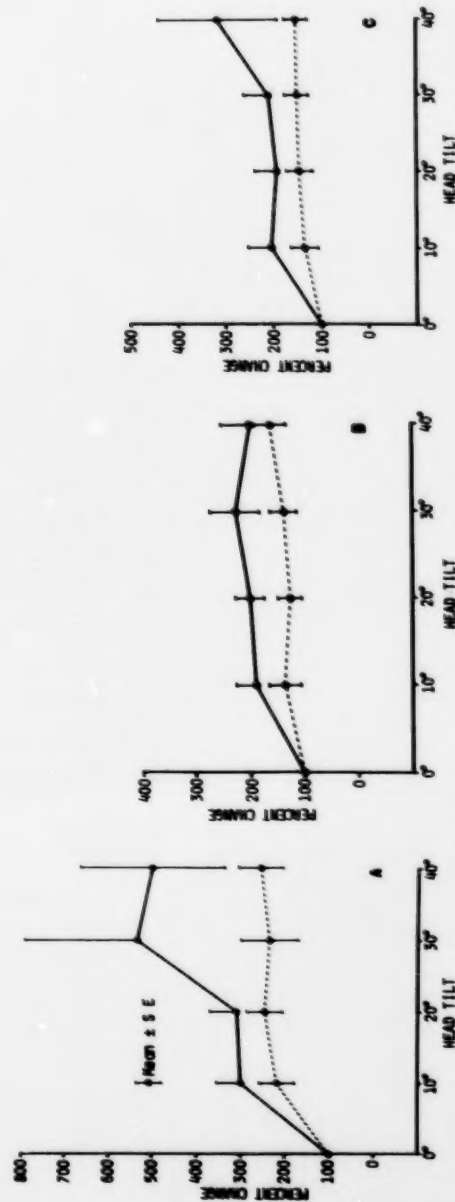


FIG. 11. Mean $\pm$ SE percentage changes in the spontaneous firing rates of the cells induced by tilts to the right or to the left. The values are related to the horizontal position (0°) and are expressed as a percentage of those rates for A—during tilt, B—1st minute after tilt, and C—5th minute after tilt. Intact cats (—); labyrinthectomized cats (---).

TABLE 5
Percentage Change in Spontaneous Activity after Successive 10° Tilts to the Right and to the Left^a

Tilt condition	Right tilt		Left tilt		Both tilts pooled	
	Controls	Labyrinthectomized	Controls	Labyrinthectomized	Controls	Labyrinthectomized
During tilt	285.3 ± 75.9	153.6 ± 13.8*	207.9 ± 20.8	199.6 ± 18.9	252.7 ± 44.8	177.2 ± 12.0*
First minute after tilt	132.6 ± 14.2	105.4 ± 13.0	108.9 ± 10.7	114.0 ± 8.8	121.1 ± 9.0	109.8 ± 7.8
Fifth minute after tilt	146.2 ± 21.0	118.0 ± 12.3	102.5 ± 7.9	119.5 ± 11.5	125.0 ± 11.6	118.7 ± 8.4

^a The values are expressed as a percentage of the immediately previous rate of spontaneous activity $\bar{x} \pm \text{SE}$.

* Statistically significant difference between control and labyrinthectomized conditions, Student's *t* test, $P < 0.05$.

large extent, from an interaction between the vestibular and visual systems. Nonvestibular sources of information concerning head orientation might be from other visual cells, proprioceptors in the neck muscles, and motor centers attempting to return the head to the upright position.

It might be argued that the changes in the positions and sizes of the receptive fields are actually artifacts resulting from deformation of the eye bulb during tilt and subsequent minor displacement of the eye in the orbit, or from minor residual compensatory movements of the eyeballs. An attempt was made to account for this, and some change in the geometry of the eyeball does take place when the head is tilted toward the studied eye. However, this displacement did not exceed 2.5% of the distance between the area centralis of the eye and the optic disc; and, therefore, it is much smaller than the observed changes. The most compelling argument in this respect is derived from the comparison between the intact and labyrinthectomized animals. If the results reported are only artifacts caused by physical factors, then there should be no differences between the two groups.

Another objection may be that these changes are induced by a nonspecific arousal induced by the unnatural position of the head of the animal. Meulders and Godfraind (16) found that reticular stimulation causes the receptive fields of the transmission cells of the lateral geniculate nucleus to become larger. Also, complex cells in the visual cortex increase their firing rate when the reticular formation is stimulated (26). However, these findings cannot explain why head tilt induces an increase in the spontaneous firing rate in some cells, but a decrease in others. The dimensions of the receptive fields also show changes in both directions. Thus, a global origin of these effects seems improbable.

Other authors, notably Horn *et al.* (6) have reported that only about 5% of the cells in the visual cortex are influenced by tilt. This study shows that, in an intact animal, all complex cells are influenced. There are several probable explanations for this discrepancy. In this study, attention was focused on the complex cells of area 18, which may respond to head tilt in a more complicated manner than the simple cells of Brodmann's area 17 studied by other authors [e.g., (27)]. The most important difference is that several measures of cell function were studied herein. Also, a more complex method for the assessment of the changes in the directional preference was used in this study.

Another factor to be considered is that Horn *et al.* (6) worked with animals anesthetized with barbiturates. Barbiturates may either limit the responsiveness of visual neurons, or decrease the number of neurons responsive to tilt. The results of Mandl *et al.* (14) as well as our work (22) indicate that even nitrous oxide, an anesthetic agent routinely used in this type of research, substantially alters the functional characteristics of visual cortical cells.

One important finding described in this paper is that the length of the receptive field, as well as the length of the path on which the light bar is able to excite the cortical cell, are not constant. After the changes in the receptive field characteristics during the tilts in both directions were analyzed, there was always one position in which the length of the optimal line, its path, and the receptive field area were smallest. From that position, the receptive field measurements increased gradually in both directions. One may speculate that, for any head position, there are some cells which will be most finely tuned to moving visual stimuli in that position. The distribution of the positions of the "minimal length," "minimal width," and "minimal area" for all head tilts indicates that the majority of cells perform optimally in nonhorizontal orientations.

In this study, it was not possible to provide an explanation of the change of the receptive field shape and dimensions induced by a head tilt. However, recently the receptive fields of the visual cortical cells were plotted by an objective, computer-assisted method (23). It was found that an increase in the receptive field area involves an increase in the number of spikes in the periphery of the receptive field where the firing before tilt was only sparse, and not detectable by the hand-held ophthalmoscope.

An open question still remains in regard to the neuronal mechanisms that are responsible for the assignment of individual cortical neurons into the "simple," "complex," or "hypercomplex" classes. It may be anticipated that these cells are actually just components of larger systems which cause the single cell to fire when the visual stimulus is in a particular part of the visual field, and that the "simplicity," or "complexity" of the cells results from activities outside these cells. The spatial integration of the input from the visual system, together with the inputs from the inner ear and from elsewhere then determine how the cells will respond.

In a recently presented paper, the analysis of some of the inputs into the complex cells of area 18 of the cortex was presented (23). It was reported that in the resting condition, cells kept active by reverberating impulses which circulate in the visual cortex. During visual stimulation, both the number of the inputs to the cells and the number of the outputs increases. These relations involve both the neighboring cells, and the cells situated outside the recorded region. Therefore, it may be anticipated that a change in the receptive field area, the main waves of the PST histogram, and the spontaneous activity during the head tilt are all a result of spatial summation of many inputs which are normally not active.

Another question is how the data related to the problem of object constancy. Several authors attempted to correlate the constancy of the visual image during the head-and-eyes movement to the recomputation of the neural represen-

tation which relies on the Fourier analysis done by neuronal circuits (25), by some kind of vaguely defined Gestalt coding (10), and so forth. Whatever will be the future model of neuronal relations determining the object constancy, it will have to take into consideration shifts of the receptive field positions, changes of the orientation specificity, dimensions of the receptive fields, and quickly shifting "spontaneous" activity of the cells involved.

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